# Invited Paper

## Sexual Selection and the Evolution of Butterfly Mating Behavior

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**Abstract.** The mating systems and courtship behavior patterns of butter-flies are examined from the perspective of sexual selection theory. Par-ticular attention is devoted to the effects of resource and female distributions on male mate-acquisition techniques and the occurrence and consequences of mate choice by males and females.

The study of butterfly mating behavior has a long history; most reports have been strictly descriptive, often anecdotal, or concerned primarily with the proximate mechanisms underlying courtship (for review: Scott, 1972; Silberglied, 1977). In the last few years, however, there has been an increasing effort to use butterflies and other insects to test current evolutionary hypotheses about the adaptive features of mating behavior (e. g. Blum and Blum, 1979; Thornhill and Alcock, 1983). The theory of sexual selection has been a guiding concept in this effort.

Sexual selection is the evolutionary process proposed by Darwin (1871) to explain traits whose primary function appears to be that of insuring an individual's success in courtship and mating. Of particular interest to Darwin were the elaborate secondary sexual characteristics displayed by males that in many cases seem likely to reduce a male's likelihood of sur-vival. Darwin proposed that these traits are favored by sexual selection either because they increase a male's chances of winning contests for females with other males (advantage in intrasexual competition) or because they increase a male's chances of successfully seducing a female (advantage in intersexual choice). The brilliant colors of the males found in certain species of butterflies were interpreted by Darwin as a product of sexual selection, especially intersexual choice.

Beginning with Fisher (1958), but especially in the last 10 years, there has been an attempt to formulate the theory of sexual selection more pre-cisely and to test more rigorously its predictions about male and female reproductive behavior. In this paper I will examine the mating behavior of

butterflies to see how well the observed patterns of diversity fit expectations derived from sexual selection theory and to suggest what data are needed to further test the theory.

## Sexual Differences in Butterflies

In most species of animals females and the eggs they contain are a limiting resource for males (Bateman, 1948). This is because a female typically lays relatively few eggs during her life and need only mate once or twice to fertilize those eggs. Males, on the other hand, can cheaply produce sperm sufficient to inseminate many females. It follows then that males, but not females, should be active in searching out and courting mates since their reproductive success will be limited primarily by the number of eggs they fertilize, i.e., the number of copulations they obtain.

Trivers (1972) expanded Bateman's argument by pointing out that this difference between the sexes in reproductive strategy has its roots not only in the differences between the sexes in gamete size but more generally in the differences in parental investment between the sexes. In species in which males make a substantial investment in the offspring a sex role reversal is expected of a magnitude proportional to the size of the male's investment relative to that of the female (see also:Gwynne, 1983).

In recent years it has become clear that male butterflies provide more than just sperm to their partners. During copulation the male passes into the female's reproductive tract with the sperm a sizeable quantity (about 6 percent of the male's body weight) of accessory gland secretions that probably are of nutritional value to the female. These secretions are contained mostly in a cuticle-lined sac called a spermatophore and include proteins, lipids, hydrocarbons, and water (Marshall, 1980). The protein component of the male's secretions is definitely used by the females of several species of butterflies and moths for oogenesis and somatic maintenance (Boggs, 1981; Boggs and Gilbert, 1979; Boggs and Watt, 1981; Goss, 1977; Greenfield, 1982). A case has been made that the other components might also be of use to females (Marshall, 1982a). The secretions in spermatophores have not yet been shown to increase female fitness in butterflies but such an effect of spermatophores has been demonstrated in the Orthoptera (Gwynne, 1984). Mating with its concommitant production of secretion is costly to male butterflies in that it reduces male survivorship under certain conditions (Shapiro, 1982). There has been some argument about whether these secretions constitute a true parental investment (Alexander and Borgia, 1979); it is clear, however, that their selective consequences would be the same whether they are classified as parental or mating effort (Gwynne, in press).

In spite of this investment by male butterflies, females probably make a still larger investment in terms of allocation of resources to the eggs.

Therefore, sex roles in butterflies should generally conform to the classical form (males active and competitive, females coy and passive). However, sex role reversal might occasionally be expected, especially when males are selecting mates to give their investment or when females are limited by the availability of male nutrients (Trivers, 1972).

## Butterfly Courtship and Mate Choice

Excellent summaries of the published information on butterfly courtship have been provided by Scott (1972) and Silberglied (1977) so I will here outline only the general pattern that has been observed. Once a male has located a receptive conspecific female, courtship follows in which the male is active and the female passive. If receptive and not already perched the female alights on vegetation or on the ground. The male then barrages the female with visual, chemical, and tactile stimuli by buffeting her with his wings or special scent-producing structures while flying near the female. Alternatively he may alight next to the female and perform a courtship display. In response, the female either remains motionless on the perch or extends her abdomen out from between the hindwings, thereby facilitating the act of coupling. The male then orients in a head-to-head position alongside the female and couples with her by curling his abdomen toward the female. Copulation follows and lasts from about 10 minutes to several hours (Shields and Emmel, 1973) depending in part on the average body size of the species, as shown for some pierids (Rutowski et al., 1983), and how recently the male has mated (Rutowski, 1979; Sims, 1979). During copulation the pair may engage in a post-nuptial flight either when prodded or sometimes spontaneously (Shields and Emmel, 1973). In sexually dimorphic species the sex that flies carrying the other generally has a coloration that more readily deters approaches and contacts by either conspecific males or predators (Rutowski, 1978b).

During courtship, the participants acquire information that is used in evaluating each other's potential as a mate. When copulation commits both males and females to metabolically costly investments sexual selection theory predicts that both sexes should engage in intersexual choice, that is, both should be sensitive to the quality, relative to conspecifics, of a potential mate. Females should be especially sensitive to a male's ability to produce secretions and males should be especially sensitive to female's ability to use the secretions profitably from their perspective (Rutowski, 1982a). This leads to two predictions. (1) Females should select among males on the basis of traits indicating that they can provide a large nutrient investment (Thornhill, 1976). A male's ability to produce these nutrients has been shown to be proportional to the time since he last mated and his size (Boggs, 1981; Rutowski, 1982a). Marshall (1982b) found male butterflies in the genus *Colias* collected in copulo were larger than those collected randomly. Among other traits that might be good

indicators of male quality in this regard are his age, courtship persistence, and chemical signals. Chemical signals might be especially important in that they are known to be critical for success in courtship in several species of butterflies (see Scott, 1972; Silberglied, 1977), and may be affected by larval (Grula et al., 1980) and adult diet (Schneider et al., 1975). Hence these signals might give the female critical information about the quality of a male's genes as well as the resources he has available to produce accessory gland secretions. Baker and Carde (1979) have discussed the possible role of sexual selection in the evolution of male scent-producing structures in moths.

The quality of the male's investment might be as important as its size. In ithomiine butterflies spermatophores contain defensive compounds sequestered by the male as an adult and used by the female in her own defense (Brown, 1984). These compounds are derivatives of the chemicals used in intersexual communication during the courtship (Edgar et al. 1976; Pliske, 1975a). This set of circumstances may be a product of sexual selection by females for males with chemical signals that indicate their supply of such compounds. A similar hypothesis has been proposed in Eisner (1980) and Conner et al. (1981) to explain the similarity between defensive compounds and male courtship pheromones in some other lepidopterans.

Female choice and its adaptive basis have yet to be directly tested in the butterflies although it is frequently invoked to explain phenomena such as female-limited mimicry. Turner (1978) has reviewed the literature on female-limited mimicry and analyzed the various explanations for the absence of a mimetic morph in males of species such as *Papilio glaucus* and *Speyeria diana.* He found sexual selection to be the most consistent with the current information on butterfly reproductive biology. Experimentation on female mate preferences will ultimately provide the best indication of the importance of mate choice in shaping male coloration. For example, Silberglied and Taylor (1978) have shown that females of the alfalfa butterfly *(Colias eurytheme)* mate preferentially with males whose wings reflect ultraviolet light, while the mate preferences of its congener *(C. philodice)* are not influenced by the presence of ultraviolet reflectance. Not surprisingly, the wing of *C. eurytheme* males strongly reflect ultraviolet while the wings of *C. philodice* do not (Silberglied and Taylor, 1973).

(2) Males should be selective in their choice of mates or at least their choice of courtship partner. If males are limited in their ability to produce these secretions then they should be choosy about who gets them. Marshall (1982b) found that females in field-collected mated pairs were heavier than females in a random sample from the same population. I have shown that males of the checkered white butterfly (*Pieris protodice*) preferentially court young females and large females (Rutowski, 1982b). Both these groups of females are expected to yield larger returns on the

male's investment than older or smaller mates. Young females have a longer life expectancy and female fecundity is related to size (Suzuki, 1978; Lederhouse, 1981). However, these are not absolute mating preferences for males will mate with highly receptive old or small females. But because they are less persistent in encounters with old or small females, this suggests that their behavior is structured in a way that reflects the costs and limitations of producing their investment.

While the information reviewed above suggests that mate choice may be occurring in butterflies a critical question surrounds its likely evolutionary significance. Do ecological circumstances in butterflies ever permit females and males to engage in effective mate choice? Obviously they must provide an individual with the opportunity to examine a variety of conspecifics without incurring undue costs in the form of time wasted or missed mating opportunities (Janetos, 1980). These costs will be minimized in species like *Colias eurytheme* and *Pieris protodice* that occur in relatively high density and whose flight seasons are not highly contracted, conditions that will not be met for all species of butterflies. Optimal conditions for choice are also not likely to be met at all times as density varies during a species' flight season.

### Comparative Courtship and Investment Patterns

The nutrient investment made by male butterflies appears to have given rise to selection pressures that in turn have shaped the courtship behavior of males and perhaps females. However, the data that support this notion come primarily from a few species of butterflies in the pierid family. To what extent can these results be generalized to members of other families? Does interspecific variation in behavior reflect interspecific variation in investment? Obviously, this depends on a knowledge not only of the behavior of other species but also on a knowledge of the investments made by their males.

Male behavior in courtship varies among species (for review:Scott, 1972; Silberglied, 1977). At one extreme the male buffets the female briefly by flying about near her before alighting and attempting copulation. In the other extreme, the male performs special displays such as the bowing display of the grayling male (*Eumenis semele*, Tinbergen et al., 1943), the hairpencilling display of danaid males (Brower et al., 1965; Pliske, 1975b) or the wing waving display of *Eurema daira* males (Rutowski, 1983). During courtship a male grayling stands facing a perched female, bows forward, and clasps her antennae between his wings. The antennae, thereby, contact presumptive scent-producing scales on the male's wings. In danaid butterflies the male flies up and down in front of flying and perched females in a way that brings special scent-producing structures called hairpencils at the end of his abdomen into contact with the female's antennae. The barred sulphur (*E. daira*)

male alights next to a perched female and courts her by waving his fore-wing on the side next to the female up and down in front of her, actually rubbing the trailing edge of the wing along the length of the female's antenna with each upsweep.

These differences seem to be modest variations on a basic courtship plan found throughout the butterflies. The general lack of interspecific variation in the complexity of successful courtship suggests that interspecific variation in the magnitude of the investment made by males will be small. In contrast, Gwynne (1983) has observed a variety of courtship patterns in the Orthoptera that range from the standard male-male competition for females to situations in which females fight among themselves for access to males. In the species he observed, males pass nutrients to females at copulation and those species that display sex role reversal are those in which the male provides the female with huge quantities of secretion at mating, up to 20% of the male's body weight and more.

Recently, my coworkers and I surveyed the size of the investment made by males of ten species relative to their body weight and the body weight of conspecific females (Rutowski et al., 1983). The ten species included 5 pierids, 3 nymphalids, one papilionid, and one lycaenid. The courtships of these species are all similar in overall form. The results indicate a strong similarity from species to species in the quantity of nutrients passed by the male during copulation relative to his body weight. The size of the male's investment is consistently about 6% of his body weight. We conclude that these data support expectations from theory but acknowledge that some currently untested assumptions underlie this conclusion. Students of the mating behavior of butterflies and moths should pay special attention to species whose males exhibit unusually complex mating patterns or produce usually large or small nutrient investments.

These observations suggest that the diversity of courtship displays and signals found in butterflies is not a result of interspecific differences in the intensity of sexual selection but instead a result of differences in the direction of sexual selection favoring males that clearly announce their species identity or other characteristics that might enhance female reproductive success. That announcement of species identity is an important aspect of these displays is supported by the variation in courtship behavior observed in a complex of three small sulphurs, *Eurema daira, E. lisa,* and *Nathalis iole*, that are sympatric in the Neotropics and interact frequently. These species are similar in color; but, both *E. daira* and *N. iole* have a black bar along the trailing edge of the dorsal forewing that is not present in *E. lisa*. I have already described the wing-waving display of *E. daira,* and *N. iole* has a wing spread display that is dramatically different in form (Rutowski, 1981). In *E. lisa,* the male buffets the female with his wings in a non-specific way during the courtship (Rutowski, 1978b). Interestingly, the species most similar in coloration have the most

distinctive and pronounced displays. Suzuki et al. (1977) found a well-developed diversity in the courtship behavior of four similar species of *Pieris* sympatric in Japan. In mimetic complexes in which sexual and species discrimination by males and females might be a special problem as well as in complexes of similarly-colored sympatric relatives it is expected that male courtship signals and displays should be particularly divergent.

## Female Mating Systems

Although female butterflies sometimes will mate multiply, as a rule they mate only one or a few times during their life (Burns, 1968; Ehrlich and Ehrlich, 1978; Pliske, 1973), and at widely spaced intervals (Suzuki, 1979). During their lives females are faced with the conflicting demands of mating, feeding, and ovipositing. A single copulation may take up a substantial percentage of the daylight hours during which temperatures are appropriate for flight. Copulation may have other costs as well such as exposure to predation. Time limitation on female reproductive output has been demonstrated for *Anthocaris cardamines* by Courtney and Duggan (1983) and for *Colias alexandra* by Hayes (1981) and suggested for other species by Rutowski (1978) and Wiklund (1982). Oviposition sites are characteristically widely scattered in space and females of most species deposit only a small complement of their total output of eggs at each oviposition site (Stamp, 1980). Egg dispersion maybe favored to reduce parasite infestations and overuse of larval resources. Nectar resources are similarly widely scattered, may not occur in the same areas as oviposition sites, and provide only a small quantity of material each time the female alights.

These observations lead to three predictions about female reproductive behavior in butterflies. First, mated females should be generally refractory to copulatory attempts in order to maximize time available for oviposition and feeding. This is in fact the case. Between matings females display a great reluctance to mate and a variety of movements and postures that mechanically impede male copulatory attempts. These include flutter responses (e.g. Rutowski, 1978b), mate refusal postures (e.g. Obara 1964b), and ascending flights that curtail male courtship attempts (Rutowski, 1978a). Both mechanical and hormonal cues initiated by the inflation of the bursa may be responsible for the initiation and maintenance of the female's refractory state (Sugawara, 1979; Obara, 1982). In heliconiine butterflies, females may use a chemical signal or antiaphrodisiac that is obtained from males during copulation to discourage the courtship attempts of other males (Gilbert, 1976). All of these behavior patterns may benefit a successful male by insuring that eggs produced using his nutrients are fertilized with his sperm. Last male precedence has been shown in several lepidopterans (Gwynne, in press).

Second, female butterflies should remate only when their supply of secretions or sperm from previous matings is depleted (Suzuki, 1979; Lederhouse, 1981). This appears to be the case in that the first-deposited spermatophore in twice-mated females is usually in a highly collapsed state (Rutowski et al., 1981). Studies of the patterns of female receptivity as related to supplies of sperm and male-imparted secretion are badly needed. Third, given that the secretions received from males are of nutritional importance to females, and that males are to some extent selective about who gets their secretions females are expected to sometimes play an active role in courtship. In fact, female butterflies have been observed to actively approach and chase males (courtship solicitation) especially when they are virgin (Wiklund, 1982) or when their supply of secretions from previous matings is depleted (Rutowski, 1980; Rutowski et al., 1982).

## Male Mating Systems

Male butterflies are not monogamous but will mate repeatedly, even on the same day, if given the chance (Sims, 1979, Rutowski, 1979). Hence, polygyny best describes the typical male butterfly mating system. Emlen and Oring (1977) presented a model recently expanded by Thornhill and Alcock (1983) that relates the structure of animal mating systems to certain key ecological variables. They point out that in polygynous mating systems in which males display more or less classic sex roles, the strategies used by males to maximize contacts with females will be determined by (1) the distribution of receptive females in the environment and (2) the ratio of receptive males to receptive females, that is, the operational sex ratio. In the remainder of this paper I will present the predicted relationships between male mating system structure and these ecological variables and examine the extent to which butterfly mating systems do or do not fit the predictions.

**Female- and Resource-Defense Polygyny.** Emlen and Oring focus on the extent to which males can monopolize mates either through direct defense or through defense of resources of interest to females. If males can economically monopolize females by protecting them from the attentions of other males either in groups or individually in series female-defense polygyny will evolve. In butterflies no species is known in which females form defensible sex-specific groupings. In addition females become refractory after mating and remain so for some time. These factors will limit the benefits males may gain from female defense and suggest that this behavior will be rare in butterflies. No clear examples of female defense are known in the butterflies. However, in *Heliconius erato* the potential for such a mating system is strong in that males locate preemergent females using a chemical emitted by the pupae (Bellinger, 1954). Males might well defend these pupae. Why the pupae emits such a signal is unclear.

Males may also monopolize females by defending resources of interest to females and thereby gain exclusive copulation rights to females when they visit the resources. In the ecological circumstances that favor this system the resource of interest to females is clumped in a way that permits a male to be guaranteed frequent contacts with receptive females but to minimize time and energy in defense of the resource. In butterflies the primary resources of interest to females are nectar sources and oviposition sites. These resources are typically represented by small annual plants that are too widely dispersed to assure frequent visits by females many of which are likely to be unreceptive. Hence this mating system is also expected to be relatively rare in butterflies. When it does occur the resources should be found in clumps that are economically defensible and not too abundant, such as small trees and bushes.

As with female-defense polygyny, potential examples of resource-defense polygyny are rare as expected. Two cases stand out in which site defense appears to be closely tied to the location of appropriately structured resources. First males of *Papilio indra minori* participate in dramatic fights near service berry bushes, the prime nectar source for this butterfly in the region where the fights were observed (Eff, 1962). The hackberry butterfly, *Asterocampa leilia*, feeds as a larva on hackberry trees (*Celtis* spp.) which are characteristically small in stature. Males perch along washes and apparently defend stretches of the wash. Austin (1977) found that all such territories contained hackberry trees which might be prime locations for encountering ovipositing females. The hackberry trees would also be prime locations for encountering newly-emerged virgin females and so their defense might also constitute female-defense polygyny.

In some cases male butterflies also appear to be engaging in resource-defense polygyny but the resources are less obvious than oviposition sites or nectar sources. Males of the speckled wood butterfly (*Parage aegeria*) defend sun spots on the forest floor that Parker (1978) has suggested may be a thermoregulatory resource for ovipositing females. Davies (1978) in one of the most detailed studies of site defense in a butterfly has shown that males that defend sun spots have more frequent contacts with females than do males in other parts of the habitat. Wickman and Wiklund (1983) have confirmed many but not all of Davies' results and also shown that the intensity of sunspot defense increases with the likelihood of visits by females. In most of the territorial species discussed here the contests between males take the form of spiral, ascending flights.

**Pure Dominance or Lek Polygyny.** Resource defense mating systems are expected to evolve when a balance is struck between the arrival rate of receptive females and the density of would-be territory owners. If this balance is not met then mate monopolization potential is low and other types of mating systems are expected to evolve, either pure dominance

polygyny or scramble competition polygyny.

Male dominance or lek polygyny is only expected when the distribution of females in time and space is extremely widespread. Under these conditions selection may favor the evolution of traditional mating sites that are not based on any resources of interest to the female (Bradbury, 1981). At such sites males are expected to aggregate and may defend territories in anticipation of visits by receptive females. If territories are defended at these traditional mating sites they will not be centered on any resource of interest to the female and the aggregation of males is referred to as a lek.

The defense of hilltop territories by male butterflies is well known to butterfly collectors and students of butterfly behavior (see Shields, 1967), and clearly supports the expected relationship between lek polygyny and ecological variables. Typically the most hotly contested territories are those nearest the top of the hill and contain neither larval foodplants nor nectar resources. Lederhouse (1982) has documented hilltopping behavior in the black swallowtail, *Papilio polyxenes*. As well as showing that males are territorial on hilltops he has shown that the highest territories are most likely to be visited by receptive females and intruding males and most actively defended. A similar relationship between territory position and attractiveness to males has been shown for the great purple hairstreak, *Atlides halesus* (Alcock, 1983). In both *P. polyxenes* and *A. halesus*, as expected, the food resources are widely distributed and the flight season is very protracted, often lasting several months (Lederhouse, 1982; Alcock, 1983).

The symbolic territories that characterize leks need not be contiguous. In such situations the lek territories are dispersed and most likely to occur in areas where males can get the best view of passing females or in areas females are likely to visit due to habitat structure. In *Heodes virgaureae* (Douwes, 1975), *Inachis io, Aglais urticae* (Baker, 1972), *Incisalia iroides* (Powell, 1968), *Precis coenia* (Scott, 1975a; Hafernik, 1982), *Lasiommata megera* (Dennis, 1982), *Vanessa atalanta* (Bitzer and Shaw, 1979), *Nymphalis antiopa*, and *Polygonia comma* (Bitzer and Shaw, 1983), males occupy and apparently defend for several days sites that have been described as being along wood margins, along paths, in ravines, or in bare areas. As an alternative interpretation such areas could be construed as resources in the form of space for optimal movement through the environment and, hence, the behavior of the males could be taken as resource defense polygyny. In either case, the ecological circumstances expected to give rise to such a mating system would be similar.

At this point it is appropriate to make four comments on territoriality in butterflies. First, the occurrence of territoriality in butterflies has been disputed (Scott, 1974; Suzuki, 1976) largely because of difficulty in distinguishing sexually motivated chases from aggressive chases and because the lack of an obvious resource near a male's perching site. More

recent studies (see especially Wickman and Wiklund, 1983) firmly document that territoriality and aggression do occur in butterflies. Second, territorial behavior no doubt intergrades into non-territorial behavior within and between species. In some species perching sites appear quite labile in time and space (Scott, 1975a; Hafernik, 1982; Suzuki, 1976). Third, observations of territorial behavior have generally been lumped under the name of perching or waiting by males for purposes of mate location (Scott, 1974, 1975b, 1982). The scheme presented here helps understand the variation in territorial behavior and the ecological circumstances that favor such behavior. More detailed studies of perching are needed that focus on the relationship between male behavior, resources, females, and the spacing of individuals in the environment. Finally, males engaged in contests for access to females are subject to intrasexual selection for traits that maximize success in such contests. This type of selection has been promulgated by Silberglied (in press) as an alternative to intersexual mate choice used by Darwin (1871) as an explanation for the brilliant color found on males but not females of some species of butterflies.

Alcock (in press) has also found that some hilltopping butterflies are non-territorial and only patrol the hilltop. He like Parker (1978) has suggested that such behavior will be most advantageous when the ecological circumstance favor traditional mating sites but the density of conspecific males at the site is too low or too high to make exclusion of conspecifics profitable at these sites. If there are only a few males on the hill, territoriality makes little sense for individuals; if there are many males on the hill the energetic costs of excluding them will make territoriality disadvantageous.

*Scramble Competition Polygyny.* Abundant but not patchily distributed resources and short flight seasons will favor males that do not engage in contest competition with other males for females at resources or leks but that instead fly about the environment searching for receptive females in a scramble competition with other males. Two types of scramble competition polygyny have been proposed.

When receptive females are highly concentrated in time and space males should aggregate in high density when and where these aggregations are likely to occur. Emlen and Oring have called these aggregations explosive breeding assemblages. Such concentrations of receptive females are not likely to be common in butterflies but the mating frenzy of monarch butterflies (*Danaus plexippus*) that occurs just before they disperse from their winter aggregations may qualify as an explosive breeding assemblage. Females in these aggregations become receptive during the days before they disperse in the spring and during this time males fly about courting females and mating with any that will have them (Hill et al., 1976; Brower et al., 1977). Also, concentrations of reproductively active non-territorial males near food sources have been described for

*Eumenis semele* (Tinbergen et al., 1942) and *Perrhybris pyrrha* (DeVries, 1978).

Thornhill and Alcock have suggested that prolonged searching polygyny will evolve when none of the conditions discussed above are met. Males then are expected to fly about broadly in search of receptive females in an effort to outrace their competitors. From the information and analysis given above this is perhaps the most likely mating system to be found in butterflies. It is the most commonly reported form of butterfly mating-locating behavior reported in surveys by Scott (1974, 1975b, 1982). Males engaged in scramble competition for mates characteristically fly rapidly through the environment and investigate anything they contact that even remotely resembles a female. Such males are often seen to closely investigate larval foodplants where they may encounter newly emerged virgin or receptive ovipositing females.

There are two additional comments on sexual selection and male mating systems in butterflies. First, competition for access to females has frequently been invoked to explain the observation that in any given flight season males typically eclose earlier than females. This is called protandry and several theoretical and empirical analyses support an intrasexual competition explanation (Wiklund and Fagerstrom, 1977; Wiklund and Solbreck, 1982; Iwasa et al., 1983; Parker and Courtney, 1983). Furthermore, Singer (1982) has presented data suggesting that males in univoltine species with restricted flight seasons may be under more intense sexual selection for protandry and therefore may, as a result of the required rapid development, be smaller than females than males in, for example, multivoltine species (see also, Lederhouse, et al., 1982). Second, although this discussion has focused on interspecific differences in male mate acquisition strategies, variation in mating system structure may also occur within species. The possibility of such variation has been discussed by Scott (1974, 1982) who cited a number of species in which males patrolled in some areas and perched in others. Male mate-locating behavior also varied with time. He focused on the role of population density in determining the optimum mate-location strategy. Dennis (1982) has documented changes from patrolling to site defense in the wall brown (*Lasiommata megera*) and attributes the change to changes in resource distribution as well as density. Investigators of butterfly mating systems should be sensitive to the fact that as in other species of insects intraspecific variation in male mating behavior may occur along the axes of male size (Alcock et al., 1977), time of day (Marshall, 1982b), population density (Cade, 1979), or other relevant ecological variables.

The existing information on butterfly mating systems appears to provide preliminary support for the theoretical relationships predicted by sexual selection theory between mating system structure and various ecological variables, especially the distribution of females and the operational sex ratio as both are influenced by female mating and

emergence patterns. However, there is much more to be done. Quantitative assessments of female and resource distribution, and careful comparative studies of detailed case histories will go far toward establishing the accuracy of these correlations.

## Summary

Clearly, the most robust tests of sexual selection theory will come from testing explicit predictions drawn from it using butterflies and other organisms. Butterflies appear to be particularly suitable for tests of predictions about sexual differences and mating systems because of the unusual nature of male nutrient contributions made during mating and because of the diversity in male mating behavior found both within and between species. I hope this article serves to introduce some of this potential to butterfly biologists and stimulates additional interest in the adaptive features of the sexual behavior of these beautiful and behaviorally diverse organisms.

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